SEED-BANKS IN TWO REMNANT RESERVES OF CONTRASTING LOCATION, ECOLOGY AND MANAGEMENT HISTORY IN SOUTH-WESTERN AUSTRALIA.

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ABSTRACT

The assessment of the health of remnant fragments of bushland is often based on subjective observations, particularly using the status of above ground vegetation. In areas long unburnt, a vital contributor to the regenerative potential is a healthy soil seed-bank that can germinate following a major perturbation. Germination trials were conducted from the soil seed-banks of two remnant reserves of contrasting location, ecology and management history near Goomalling and Bunbury, to determine their respective regenerative potential and to compare the soil-seed species to the above ground vegetation. Both reserves retained a soil seed bank in the topsoil, indicating some regenerative potential. Differences in vegetation composition overall were concentrated in non-bradysporous species, particularly in the understorey and ground layers. Annuals dominated the predominant herbaceous layer at the drier wheatbelt site and perennial herbs and shrubs were more profuse at the site on the moister Swan Coastal Plain. There is a clear need to tailor reserve management and restoration to local biological circumstances in south-west Australian landscapes, more so than most other places on earth.

INTRODUCTION

South-western Australia encompasses a wide array of ecosystem types, ranging from closed forests on the southern fringes of the south-west to shrublands and open woodlands as one progresses in an easterly and north-easterly direction (Beard 1990; Hobbs 1992). Diverse vegetation communities and great species richness within these systems are the end-products of long and complex evolutionary processes (Hopper 1992; Hopper *et al.* 1996). More recently, a number of variables may drive the basic differences between and within ecosystem types. One of the more influential of these variables is rainfall, which decreases from an annual average of 1500 mm in the extreme south-west (Gentilli 1989) to about 250 mm at the edge of the arid interior of Western

Australia (Hobbs 1992). Indeed, Hopper (1979) suggested a system of phytogeographic divisions in the south-west based on rainfall, with a High Rainfall Zone encompassing areas of 800 – 1500 mm annual rainfall in the extreme south-west, a Transitional Rainfall Zone covering areas of 300-800 mm annual rainfall including the wheatbelt, and an Arid Zone of less than 300 mm annual rainfall further inland (see Figure 1 in Saffer 2002). Furthermore, the periodicity of rainfall influences the life form of vegetation, with fewer raindays conducive to annuals and herbs, and longer periods of rain supporting relatively more perennials and shrubs (Beard 1990).

The combination of complex soil mosaics and climatic influences in the south-west, combined with intrinsic rarity and population isolation, have resulted in great species diversity, high levels of endemism and a remarkable turnover of species across the landscape over relatively small distances (Hopper 1992; Hobbs and Saunders 1993; Myers *et al.* 2000). Clearing of these native landscapes for agriculture, mining and urbanisation, and the neglect and degradation of remaining tracts of native vegetation in the south-west are recognized and well documented. Restoration processes have been initiated that now identify, for example, the importance of provenance in regeneration (Handel *et al.* 1994; Coates and van Leeuwen 1997) or the importance of topsoil management on disturbed sites (Rokich *et al.* 2000).

The two natural seed stores in regenerative processes are bradysporous or canopy-stored seed, (also known as serotinous), and soil seed-banks (Bell *et al.* 1993; Baskin and Baskin 1998). There is increasing concern that most, and in some areas, all, local indigenous bradysporous seed available has been harvested by seed collectors (Mortlock 2000). The soil seed-bank, when managed proficiently, is the most valuable resource for the rehabilitation of land following clearing (Dixon and Meney 1994; Ward *et al.* 1996; Bellairs and Koch 1999; Read *et al.* 2000; Smith *et al.* 2000). Indeed, the top 5 cm of topsoil in a 30 cm profile may contain more than 90% of seed stored in the soil (Rokich *et al.* 2000). The re-establishment of a diverse assembly of native species in the rehabilitation of mined lands is invariably associated with the importance of the soil seed-bank, and the handling of the topsoil (Dixon and Meney 1994; Bellairs and Koch 1999; Rokich *et al.* 2000; Smith *et al.* 2000). The value of the soil seed-bank in remnant vegetation and its regenerative potential in these remaining patches has received far less attention.

In the wheatbelt area of south-western Australia, woodlands have been almost completely eliminated from the landscape, with as little as 3% of some types remaining (Beard and Sprenger 1984; Hobbs 1999). Although legislation has slowed the rate of further clearing of native vegetation, remaining patches remain susceptible to other forms of disturbance, such as invasion of exotic species from adjacent areas, and fire. Landscape fragmentation and weed invasion also alter ecosystem processes within remnant patches, resulting in further habitat decline and species loss (Panetta and Hopkins 1991; Saunders *et al.* 1991; Hobbs 1993; Smith *et al.* 1996; Williams and West 2000). The self-sustainability of remaining, isolated patches of remnant vegetation is paramount to their survival. While the sparsity of remnant patches in the wheatbelt accentuates their vulnerability to further degradation, other remnants, such as those in the Swan Coastal Plain, are similarly subject to the debilitating effects of invasions, deleterious natural elements and loss of biodiversity and, therefore, loss of sustainability.

This study assesses and compares the soil seed-banks of two reserves of remnant vegetation of contrasting ecology and management history in the south-west of Western Australia. The composition, abundance and distribution of seeds in the topsoil of two reserves, one inland and one coastal, were determined as a means of assessing the regenerative potential of each reserve. Comparisons were made within and between the reserves examining species in the soil seed-banks and species present in the above ground vegetation.

THE GOOMALLING AND FRANKLANDIA RESERVES

The Goomalling Reserve or Reserve 1562 (hereafter referred to as Goomalling) (31°16'S, 116°47'E) (120 hectares) is located within the wheatbelt approximately 1km east of the township of Goomalling and 160km NE of Perth (see Figure 1 in Saffer 2002). Average annual rainfall is approximately 370 mm with rain falling on a mean of 82.5 days per year (Bureau of Meteorology, Perth, WA). Soils are heavy clay loams and support vegetation which consists of a mixed eucalypt woodland with *Eucalyptus loxophleba* (York Gum), *E. salubris* (Gimlet), *E. salmonophloia* (Salmon Gum) and *E. longicornis* (Red Morrel) dominating with an open understorey. The current status of this reserve is for 'Travellers and Stock'. However, it has not had stock on it for at least 80 years. The reserve is surrounded by agricultural land (wheat fields) to the north and north-east, a disturbed woodland to the west, and a major road forms the remaining boundary. There has not been a fire on the reserve for at least 80 years, it is unfenced, and has never been actively managed. Indiscriminate vehicle and trail bike tracks traverse the reserve and evidence remains of past and present timber collection and dumping of soil and other refuse.

Franklandia Reserve or Reserve A1167 (hereafter referred to as Franklandia) (33°25'S, 115°42'E) (19.56 hectares) is located near the south-west coast of Western Australia within the Swan Coastal Plain, approximately 14 km south-, south-east of Bunbury (see Figure 1 in Saffer 2002). Average annual rainfall is approximately 900 mm with rain falling on a mean of 122.3 days per year (Bureau of Meteorology, Perth, WA). Soils are deep sands and vegetation consists of jarrah and banksia woodland with a moderately to highly dense understorey. Its official purpose is designated as 'Parklands'. The reserve is surrounded by agricultural land to the north and south: anecdotal evidence suggests that cattle on these farms may have entered and grazed for short periods when fences on these boundaries were in need of repair. The farm to the west had been cleared but subsequently allowed to regenerate and a major road forms the eastern boundary. Small, contained fires occurred in sections of the reserve in 1981, 1995 and 1996. The reserve is managed by the

Department of Land Administration, the Department of Conservation and Land Management and, in 1995 members of the Bunbury Naturalists' Club became official caretakers. At that time, members of the Bunbury Naturalists' Club removed 13 car bodies from the reserve and approximately 20 m^3 of rubbish. Fencing around the entire reserve was secured, and locked gates were erected allowing only authorized vehicular access. Pedestrians have free access. Tracks that traversed the reserve have been allowed to regenerate and the monitoring of flora and removal of rubbish is on-going.

Based on the different locations, ecology and management regimes of the two reserves, a number of hypotheses were investigated. The irregularity and small scale of cattle invasion and fires at Franklandia, in addition to the distances of these perturbations from the soil seed-bank collection sites, did not warrant their inclusion in the hypotheses and they were not considered further in this study.

Hypothesis 1: Lower rainfall and fewer raindays at Goomalling, preventing seeds in the soil from access to water, an essential germination cue, would result in a larger soil seed-bank, evident as a greater number of germinants in the topsoil from Goomalling than from Franklandia.

Hypothesis 2: Irrespective of the location, ecology or management of vegetated sites, seed density would be greatest in the top layer within the soil profile and would decrease with increasing depth (see Rokich *et al.* 2000).

Hypothesis 3: The eucalypt woodland with open understorey at Goomalling would support a greater herbaceous layer than at Franklandia, while the jarrah-banksia woodland with a denser understorey at Franklandia would support a greater shrub layer than at Goomalling.

Hypothesis 4: Within the herbaceous layer, there would be relatively more perennials than annuals in the greater rainfall area of Franklandia than at Goomalling and, conversely, annuals would be relatively more abundant than perennials at Goomalling, with lesser rainfall, compared to Franklandia.

Hypothesis 5: Lack of management and greater disturbance at Goomalling would result in higher numbers of non-native species invading from surrounding wheat fields compared to Franklandia, which is better managed and is surrounded by cattle farms.

METHODOLOGY

VEGETATION SURVEY

At each reserve, four sites (30 m x 30 m) were selected in vegetation representative of the dominant vegetation in each reserve as part of a larger study (Saffer 2002). Species lists based on intensive sampling over all seasons across two years are provided for all sites in both reserves (See Appendices 1 and 2). Nomenclature follows Paczkowska and Chapman (2000).

SOIL SAMPLING

At each of the four marked sites in each reserve, 10 soil samples were collected: a soil core of 20 cm by 20 cm was removed at depths of 0-2 cm and 2-5 cm per sample. Two depths were selected to determine the depth in which the majority of seeds occur: previous studies have shown a decline in seed density with increasing depth in soil profile (Tacey and Glossop 1980; Rokich *et al.* 2000). Soil samples were placed separately in individually labeled calico bags and stored in a cool room until further analysis. Soil samples were collected from each reserve in March 2000, to coincide with cool autumn temperatures (see Rokich *et al.* 2000).

GERMINATION TRIALS

Germination trials commenced at the beginning of April 2000, within two weeks of the soil collections. Sterilized trays (30 cm x 35 cm x 4 cm) were lined with perforated cloth and filled to a depth of 3cm with pasteurised silica sand. Each soil sample was removed from the individually labeled calico bags and sieved (3.35 mm mesh-size aperture) to remove large rocks, twigs and other large biomass. The sieved sample was spread to a depth of 1cm over the silica sand. Samples collected from 2-5 cm often required more than one tray per sample. All trays were treated with a soil conditioning agent (Wettasoil©) to ensure even saturation, and were then watered thoroughly. The trays were placed on shelves in a steel-framed tent and exposed to aerosol smoke treatment for one hour, as described by Dixon *et al.* (1995). It has been established that smoke elicits a significant germination response in many Western Australian native plants (Dixon *et al.* 1995; Roche *et al.* 1997; Lloyd *et al.* 2000). After treatment, the trays were placed randomly inside a greenhouse and were watered as required. The emergence of vascular plants was recorded weekly for a period of 20 weeks. Germinants were grown until they could be identified and were then removed from the trays to reduce competition and the risk of fungal contamination. Although the actual area sampled in each reserve was 6.4 m^{-2}, seed density was also determined as number of seeds per square metre for comparison with published studies.

RESULTS

ABOVEGROUND VEGETATION

For Goomalling, 44 native species were recorded in 30 genera from 17 families, and five species in five genera from two families were listed as non-natives (Appendix 1). Native species in Franklandia totalled 111 species in 72 genera from 28 families with *Briza maxima* (Poaceae) and *Disa bracteata* (Orchidaceae) the only non-native species present above ground (Appendix 2).

SOIL SEED-BANKS

The total number of germinants from Goomalling was more than two-fold greater than the total number from Franklandia (Table 1). Twelve species from Goomalling and seven from Franklandia, of which two were common to both, died before being positively identified. Native species accounted for 70% and 61% of all species in Goomalling and Franklandia respectively. Nevertheless, the distribution of native to non-natives species was similar in both Goomalling and Franklandia in terms of the number of germinants (t_2=0.747, P = 0.532) and the number of species (t_2=0.428 P = 0.710) (Table 1, Appendix 1 and 2).

Table 1. Number of germinants, species, families and genera from soil seed-banks at Goomalling and Franklandia reserves.

	Goomalling	Franklandia
Total number of germinants	8024	3897
Number per m^2	1253.8	608.9
Native	5610 (70%)	2364 (61%)
Non-native	1361 (17%)	1342 (34%)
Unidentified	1053 (13%)	191 (5%)
Total number of species	75	60
Native	48	44
Non-native	27	16
Total number of families	27	24
Native	19	21
Non-native	10	6
Total number of genera	53	46
Native	32	34
Non-native	20	13

Twenty-seven families were recorded from the topsoil collected at Goomalling: 19 families of native species and 10 families of non-native species (Table 1, Appendix 1). Within the native families, Crassulaceae was most frequently represented (61%): *Crassula colorata* had the greatest number of germinants (3326) overall (59%). Poaceae (70%) dominated the non-native species with *Briza maxima* (298 = 32%), *Aira caryophyllea* (230 = 25%) and *Lolium rigidum* (218 = 23%) accounting for 80% of Poaceae. Families with both natives and non-natives representatives included Asteraceae and Poaceae.

Germinants from Franklandia totalled 24 families with 21 families of native species and 6 families of non-native species. Cyperaceae, in particular *Isolepsis ossarnus* (1305 germinants totaling 97% of Cyperaceae) was recorded most often within the native species (57%), while Poaceae dominated the non-native species (87%): *Lolium rigidum* with 794 germinants accounted for 68% of Poaceae (Appendix 2). The families Cyperaceae, Asteraceae and Orchidaceae included both native and non-native species.

Most seeds (71% and 68% in Goomalling and Franklandia respectively) were present in the top 2 cm of soil rather than lower in the soil profile (2 – 5 cm) (Table 2).

Seed densities extrapolated from the number of germinants in the soil collected totalled 1254 m^{-2} for Goomalling and 609 m^{-2} for Franklandia (Table 1).

OVERALL COMPOSITION OF VEGETATION

For Goomalling, only *Enchylaena tomentosa* (Chenopodiaceae), *Eremophila drummondii* (Myoporaceae) (shrubs) and eight native herbaceous

Table 2. Total number and mean (± s.e., maximum and minimum) of germinants per tray from 0 to 2cm and 2 to 5cm soil samples from Goomalling and Franklandia reserves.

	Goomalling		Franklandia	
	0-2cm	2-5cm	0-2cm	2-5cm
Number of germinants				
Total	5707 (71%)	2317 (29%)	2653 (68%)	1244 (32%)
Number of trays	40	90	40	90
Mean germinants per tray	1426.8	579.3	663.3	311.0
s.e.	399.2	191.3	99.0	69.2
Maximum number of germinants per tray	2229	1087	908	504
Minimum number of germinants per tray	693	246	479	175

species, six of which belonged to the Asteraceae family, were present both as plants and in the soil seed-bank (Table 3). The non-native species *Ursinia anthemoides* (Asteraceae) and three Poaceae species were found both above ground and in the soil seed-bank at Goomalling.

Seven native, herbaceous species from six families were identified above and below ground in Franklandia, in addition to one shrub *Stirlingia latifolia* and one tree *Banksia attenuata* (both Proteaceae), and one orchid (*Leporella fimbriata*) (Table 3). *Briza maxima* (Poaceae) and *Disa bracteata* (Orchidaceae) were the only non-native species present both above ground and in the soil seed-bank.

The composition of vegetation at both reserves in terms of life forms, from species present both above ground and in the seed-banks, appears in Table 4. Eight tree species were recorded at each reserve. Three tree species at Goomalling were bradysporous and 5 non-bradysporous, with the opposite of these numbers for the eight trees species at Franklandia. Far fewer shrubs were recorded at Goomalling than at Franklandia, yet non-bradysporous species far exceeded bradysporous species at both reserves (88% and 95% respectively). Although both reserves recorded a similar number of herbaceous species overall, 74% at Goomalling were annuals and 70% at Franklandia were perennials. More non-native species were recorded at Goomalling than at Franklandia. Apart from one perennial geophyte at Goomalling (*Romulea rosea*) and *Disa bracteata* at Franklandia, all non-native species at both reserves were annual herbs.

Species common to both reserves included ten native species from seven families, 12 non-native species from four families and two unidentified species (Table 5). Apart from one perennial geophyte (*Drosera macrantha*), all the identified species common to both reserves, both native and non-native, were annual herbs. Asteraceae was the only family with representatives of both native and non-native species in both reserves.

DISCUSSION

The evolutionary and current influences

on the diverse ecosystems of south-western Western Australia are such that dominant vegetation types and species within these communities change over relatively small distances across the landscapes. Therefore, the remnant reserves examined, while fairly typical of vegetation types of their areas, may exhibit species abundance, diversity or levels of endemism not necessarily equal to that in adjacent reserves.

Comparing the germinants at both reserves, species abundance from the soil seed-banks was as predicted (Hypothesis 1) in that the lower rainfall at Goomalling, situated in the Transitional Rainfall Zone with fewer raindays, had a larger soil seed-bank, evident as a greater number of germinants from the topsoil at Goomalling than at Franklandia. Higher annual rainfall at Franklandia, (situated

Table 3. Plant species present both above ground and in the soil seed-bank at Goomalling and Franklandia reserves.

Goomalling		Franklandia	
Species	Family	Species	Family
Natives species			
Trees			
–		*Banksia attenuata*	Proteaceae
Shrubs			
Enchylaena tomentosa	Chenopodiaceae	*Stirlingia latifolia*	Proteaceae
Eremophila drummondii	Myoporaceae		
Herbs			
Drosera macrantha	Droseraceae	*Anigozanthos manglesii*	Haemodoraceae
Gilberta tenuifolia	Asteraceae	*Conostylis* sp.	Haemodoraceae
Neurachne alopecuroidea	Poaceae	*Dasypogon bromeliifolius*	Dasypogonaceae
Podolepsis lessonii	Asteraceae	*Drosera glanduligera*	Droseraceae
Podotheca gnaphalioides	Asteraceae	*Platysace compressa*	Apiaceae
Rhodanthe citrina	Asteraceae	*Stylidium brunonianum*	Stylidiaceae
Waitzia acuminata	Asteraceae	*Thysanotus patersonii*	Anthericaceae
Waitzia nitida	Asteraceae		
Orchids			
–		*Leporella fimbriata*	Orchidaceae
Non-native species			
Herbs			
Ursina anthemoides	Asteraceae	*Briza maxima*	Poaceae
Aira caryophyllea	Poaceae		
Avena barbarta	Poaceae		
Briza maxima	Poaceae		
Orchids			
–		*Disa bracteata*	Orchidaceae

in the High Rainfall Zone), and longer periods of rainfall, provided an essential germination cue, leaving fewer seeds in the topsoil layer at any one time.

Natural restoration processes in patches of remnant vegetation depend on seed stored both in the soil and in the canopy. However, most species in temperate Australian vegetation are non-bradysporous, and hence rely on

Table 4. The number and percentage of all species at Goomalling and Franklandia reserves collectively above ground and in the soil seed-banks, listed by lifeform.

	Goomalling Number of species	Goomalling %	Franklandia Number of species	Franklandia %
Native species				
Trees				
Bradysporous	3	37.5	5	62.5
Non-bradysporous	5	62.5	3	37.5
Sub-total and percentage of native taxa	8	9.8	8	5.6
Percentage of native and non-native taxa	6.6	4.8		
Shrubs				
Bradysporous	2	12.5	3	5.4
Non-bradysporous	14	87.5	53	94.6
Sub-total and percentage of native taxa	16	19.5	56	39.2
Percentage of native and non-native taxa	13.1	33.7		
Herbs				
Annual	43	74.1	17	28.3
Poly-ennial	0	1	1.7	
Herbaceous perennial				
Above ground	11	19.0	34	56.7
Geophyte	4	6.9	8	13.3
Sub-total and percentage of native taxa	58	70.7	60	42.0
Percentage of native and non-native taxa	47.5	36.1		
Sub-total and percentage of all native species (including orchids, cycads, grass trees).	82	67.2	143	86.1
Non-native species				
Herbs				
Annual	27	96.4	15	
Herbaceous perrenial				
Above ground	0	0		
Geophyte	1	3.6	0	
Sub-total and percentage of non-native taxa	28	100	15	93.8
Percentage of native and non-native taxa	23.0	9.0		
Sub-total and percentage of all native species (including orchids).	28	23.0	16	9.6
Total	122		166	

Table 5. Species common to both Goomalling and Franklandia reserves.

Species	Family
Natives species	
Herbs	
Perennial	
Geophyte	
Drosera macrantha	Droseraceae
Annual	
Centrolepis drummondii	Centrolepidaceae
Centrolepis aristata	Centrolepidaceae
Crassula colorata	Crassulaceae
Crassula sp.	Crassulaceae
Drosera glanduligera	Droseraceae
Isolepsis cernua	Cyperaceae
Lobelia sp.	Lobeliaceae
Millotia tenuifolia	Asteraceae
Stylidium calcaratum	Stylidiaceae
Non-native species	
Herbs	
Annual	
Aira caryophyllea	Poaceae
Arctotheca calendula	Asteraceae
Briza maxima	Poaceae
Bromus sp.	Poaceae
Hypochaeris glabra	Asteraceae
Lolium rigidum	Poaceae
Oxalis corniculata	Oxalidaceae
Sonchus oleraceus	Asteraceae
Ursinia anthemoides	Asteraceae
Vulpia myuros	Poaceae
Vulpia sp.	Poaceae
Wahlenbergia preissii	Campanulaceae
Unidentified species	
Species 4	
Species 9	

soil-stored seed for their recruitment potential (Dixon and Meney 1994). Furthermore, the predation of bradysporous seeds post dispersal, particularly by ants, certainly depletes seed on the ground (Andersen and Yen 1985; Yates *et al.* 1995). Thus, it was not surprising that there was only one bradysporous species, *Banksia attenuata*, within the tree-canopy category, that germinated from the soil seed-banks.

Of the eucalypts, *Eucalyptus salmonophloia*, for example, requires relatively high levels of disturbance such as deep ripping of soil and/or removal of adult trees for successful restoration of degraded *E. salmonophloia* woodlands (Yates *et al.* 2000, see also

Wellington 1989). Of the shrubs, while 88% and 95% of all shrubs at Goomalling and Franklandia respectively were non-bradysporous, only 28% (4 species) and 21% (11 species) of all non-bradysporous shrubs respectively, germinated.

Reasons for low numbers of germinants within the shrub layer at both reserves are unknown. The seeds were either not present in the samples, or they were present and failed to germinate. While soil samples in these germination trials were exposed to smoke and water (see Roche *et al.* 1998; Lloyd *et al.* 1999; Read *et al.* 2000; Smith *et al.* 2000), time limitations prevented the the application of heat, responsible for breaking the dormancy of many hard-coated species (Koch and Dixon 1999, Farley *et al.* 1999). The alleviation of dormancy in many Australian species is yet to be solved (Langcamp 1987; Asher and Bell 1999; Bell 1999) and may account for the low numbers.

Overall, germination of herbs yielded far greater percentages of all species at Goomalling (76%) and at Franklandia (50%), than did the shrubs or trees. Not surprisingly, fewer perennials germinated (33% at Goomalling and 33% at Franklandia) than annuals (91% at Goomalling and 94% at Franklandia). Generally, annuals are fecund, their life spans are relatively short, and most are able to put seeds back into the soil seed-bank fairly quickly, particularly in areas subject to fewer raindays. The greater number of raindays at Franklandia was more conducive to perennial growth-form. Furthermore, interactions between annuals and perennials have shown that annuals can effectively reduce or prevent perennial seedling establishment (Hobbs and Atkins 1991).

Seed densities in soils have been researched in a variety of vegetation types (see Enright and Kintrup 2001; Funes *et al.* 2001) using a variety of methods (Brown 1992) and exhibit large differences in seed-bank sizes. For example, a mean of 61 seeds m^{-2} was recorded in a Victorian *Eucalyptus regnans* forest (Wang 1997), while up to 25,000 seeds m^{-2} was reported in Californian chaparral (Zammit and Zedler 1988). Furthermore, treatments of soil samples include no treatment, heat, smoke scarification and other methods as pre-treatments of soil samples (see Enright and Kintrup 2001). Given these differences, it is difficult to make meaningful comparisons of seed densities between vegetation types and even between sites within the same area. Nevertheless, the numbers of seeds calculated in this study (1254 m^{-2} for Goomalling and 609 m^{-2} for Franklandia) fall within the range reported elsewhere.

The distribution of seed within the soil profile was similar at both Goomalling and Franklandia, with a greater percentage in the top two centimetres than between 2 and 5 cm. This is consistent with other studies that have shown a decline in seed density with increasing depth in soil profile in diverse landscapes (Tacey and Glossop 1980; Rokich *et al.* 2000), and supports Hypothesis 2.

The composition of the vegetation overall, incorporating species present in the soil seed-bank and above ground vegetation, indicates more shrubs than herbs in Franklandia, consistent in jarrah-banksia woodlands of the southwest (see Pate *et al.* 1984), and a greater herbaceous layer than shrub layer at Goomalling, characteristic of open woodlands of the drier wheatbelt (Beard 1990). Within the herbaceous layer, annuals outnumbered perennials at Goomalling and perennials outnumbered annuals at Franklandia. As suggested above, in the drier wheatbelt, the herb life form is far easier than that of a shrub, and annuals are able to sustain themselves more so than perennials, given the lower, irregular rainfall. Conversely, the heavier, more consistent rainfall at Franklandia is more conducive to a greater shrub layer and perennial herbs. This supports Hypothesis 3 which predicted the eucalyptus woodland with open understorey at Goomalling would support a greater herbaceous layer than at Franklandia, while the jarrah-banksia woodland with a denser understorey at Franklandia would support a greater shrub layer than at Goomalling. Similarly, Hypothesis 4 is supported, which suggested that within the herbaceous layer, there would be more perennials in the greater rainfall area of Franklandia than at Goomalling and, conversely, annuals would out-number perennials at Goomalling, with lesser rainfall, compared to that at Franklandia.

Invasibility of areas of remnant vegetation by non-native species depends on a number of conditions. These include proximity to non-native sources, perimeter/area ratio of the reserve with longer, more linear areas, as is the case for Franklandia, being more vulnerable to invasion than larger and broader areas, such as Goomalling (Collinge 1996; Harris 1988; Panetta and Hopkins 1991; Strawbridge 1999). Lack of management is also implicated in high numbers of non-native species within remnants, with disturbance being a major contributor. In spite of the perimeter/area ratio of Franklandia, which makes it more vulnerable to weed invasion in this respect than Goomalling, more non-native species were recorded at Goomalling in terms of number of families and number of species, than at Franklandia. General neglect of Goomalling, such as lack of fencing, indiscriminate vehicular and bike use, timber cutting and dumping are all likely contributory factors in terms of increased vulnerability to invasion by non-natives, despite the size and shape of the reserve. Furthermore, drift of fertilisers used in the adjacent wheat fields would certainly augment the growth of non-native species in the reserve. Thus, the fifth hypothesis, which implies lack of management and greater disturbance at Goomalling as a cause for higher numbers of non-native species than that at Franklandia, is supported.

CONCLUSION

This study compared the seed-banks of two reserves of remnant vegetation: one in an inland drier site with sporadic rainfall, on heavy, loamy, clay soil and the other in a higher rainfall, coastal area on leached sand. Differences in vegetation composition overall were concentrated in non-bradysporous species, particularly in the understorey and ground layers. Annuals dominated the predominant herbaceous layer at Goomalling and perennial herbs and shrubs were more profuse at Franklandia. Results indicated that both reserves contain reasonable abundances and diversity of seeds within their respective soil seed-banks, potentially sufficient to restore vegetative structure following a major perturbation such as fire. However, significant differences in soil seed-bank composition were found, highlighting the need to tailor reserve management and restoration to local biological circumstances if success is to be achieved. This is especially so in south-western Australia where turnover of plant species across landscapes is unusually rapid, more so than in most other places on earth.

While a regenerative potential is present in both reserves, the resultant landscapes following a major perturbation in each area would not necessary mirror prevailing vegetation compositions. For example, given the correct cue, long-dormant species with no current above ground representatives could germinate, and other species, presently dominant, may be temporarily excluded. The probability of non-native species flourishing before native species establish provides present land-carers with a significant challenge in terms of present and future management of their local remnant reserves. Effective removal of the current invasion and the prevention of future invasions of non-native species will go far in the restorative processes of such remaining bushlands. Management processes, such as those accomplished at Franklandia, in terms of secure fencing and prevention of indiscriminate use of the reserves, timber cutting and dumping, need to be implemented at Goomalling. Public education and public involvement in restorative process would engender an ethos of stewardship towards the land. Patches of remnant vegetation are vital in terms of conservation values, sources for restorative processes and ecosystem integrity (Dilworth *et al.* 2000). Although evolutionary processes continue to dictate many ecological outcomes, we, as temporary custodians of the few remaining patches of remnant bushland, can at least assist and influence restorative processes.

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Appendix 1. Plant species in life-form categories from Goomalling Reserve, including above ground vegetation and numbers of soil seed-bank germinants. Nomenclature follows Paczkowska and Chapman (2000).

Species	Family	Above ground P = present	Soil seed-bank Number of germinants
Native species			
Trees			
Bradysporous			
Allocasuarina huegeliana	Casuarinaceae	P	
Eucalyptus salmonophloia	Myrtaceae	P	
Hakea preissii	Proteaceae	P	
Non-bradysporous			
Acacia acuminata	Mimosaceae	P	
Acacia aestivalis	Mimosaceae	P	
Eucalyptus longicornis	Myrtaceae	P	
Eucalyptus loxophleba	Myrtaceae	P	
Eucalyptus salubris	Myrtaceae	P	
Shrubs			
Bradysporous			
Allocasuarina campestris	Casuarinaceae	P	
Allocasuarina humilis	Casuarinaceae	P	
Non-bradysporous			
Enchylaena tomentosa	Chenopodiaceae	P	2
Eremophila drummondii	Myoporaceae	P	3
Scaevola sp.	Goodeniaceae		3
Acacia sp1.	Mimosaceae		1
Acacia bidentata	Mimosaceae	P	
Acacia erinacea	Mimosaceae	P	
Acacia ligustrina	Mimosaceae	P	
Astroloma sp.	Epacridaceae	P	
Atriplex prostrata	Chenopodiaceae	P	
Bassia sp.	Chenopodiaceae	P	
Dampiera sp.	Goodeniaceae	P	
Grevillea huegelii	Proteaceae	P	
Grevillea paniculata	Proteaceae	P	
Nemcia acuta	Papilionaceae	P	
Herbs			
Perennial			
Above ground			
Conostylis aculeata subsp. *preissii*	Haemodoraceae		1
Gonocarpus nodulosus	Haloragaceae		8

Species	Family	Above ground P = present	Soil seed-bank Number of germinants
Goodenia berardiana	Goodeniaceae		1
Neurachne alopecuroidea	Poaceae	P	52
Amphipogon sp.	Poaceae	P	
Austrostipa elegantissima	Poaceae	P	
Borya sp.	Anthericaceae	P	
Conostylis sp.	Haemodoraceae	P	
Danthonia sp.	Poaceae	P	
Dianella revoluta	Phormiaceae	P	
Ptilotus drummondii	Amaranthaceae	P	
Geophyte			
Drosera macrantha	Droseraceae	P	1
Arthropodium preissii	Anthericaceae	P	
Chamaescilla corymbosa	Anthericaceae	P	
Drosera menziesii	Droseraceae	P	
Annual			
Bulbine semibarbata	Asphodelaceae		17
Calandrinia polyandra	Portulacaceae		151
Calotis hispidula	Asteraceae		21
Centrolepis aristata	Centrolepidaceae		188
Centrolepis drummondii	Centrolepidaceae		312
Centrolepis humillima	Centrolepidaceae		4
Centrolepis pilosa	Centrolepidaceae		4
Centrolepis polygyna	Centrolepidaceae		7
Ceratogyne obionoides	Asteraceae		21
Crassula closiana	Crassulaceae		21
Crassula colorata	Crassulaceae		3326
Crassula peduncularis	Crassulaceae		13
Crassula sp.	Crassulaceae		87
Drosera glanduligera	Droseraceae		11
Erymophyllum tenellum	Asteraceae		208
Gilberta tenuifolia	Asteraceae	P	56
Hydrocotyle sp1.	Apiaceae		22
Hydrocotyle sp2.	Apiaceae		12
Isolepsis cernua	Cyperaceae		36
Isolepsis marginata	Cyperaceae		5
Isolepsis ossamus	Cyperaceae		20
Isolepsis sp.	Cyperaceae		30
Lawrencella rosea	Asteraceae		4
Levenhookia stipitata	Stylidiaceae		7
Lobelia sp.	Lobeliaceae		2
Millotia tenuifolia	Asteraceae		66

Species	Family	Aboveground P = present	Soil seed-bank Number of germinants
Podolepsis lessonii	Asteraceae	P	42
Podotheca gnaphalioides	Asteraceae	P	9
Rhodanthe citrina	Asteraceae	P	23
Schoenus elegans	Cyperaceae		187
Stylidium calcaratum	Stylidiaceae		2
Stylidium ecorne	Stylidiaceae		1
Trachymene cyanopetala	Apiaceae		1
Trachymene ornata	Apiaceae		579
Trachymene pilosa	Apiaceae		9
Triglochin sp.	Juncaginaceae		2
Waitzia acuminata	Asteraceae	P	26
Waitzia nitida	Asteraceae	P	5
Brassica tournefortii	Brassicaceae	P	
Helichrysum lindleyi	Asteraceae	P	
Podolepsis capillaris	Asteraceae	P	
Rhodanthe manglesii	Asteraceae	P	
Stylidium sp.	Stylidiaceae		1
		Total	5610
Non-native species			
Herbs			
Perennial			
Geophyte			
Romulea rosea	Iridaceae		1
Annual			
Aira caryophyllea	Poaceae	P	230
Arctotheca calendula	Asteraceae		69
Avena barbata	Poaceae	P	11
Briza maxima	Poaceae	P	298
Bromus sp.1	Poaceae		19
Bromus sp.2	Poaceae		1
Fumaria parviflora	Fumariaceae		3
Hypochaeris glabra	Asteraceae		109
Juncus bufonius	Juncaceae		1
Juncus capitatus	Juncaceae		1
Juncus sp.	Juncaceae		1
Lolium rigidum	Poaceae		218
Oxalis corniculata	Oxalidaceae		18
Parentucellia latifolia	Scrophulariaceae		51
Pentaschistis airodes	Poaceae		14
Plantago hispida	Plantaginaceae		19
Poaceae sp.	Poaceae		21
Sebaea ovata	Gentianaceae		4

Species	Family	Above ground	Soil seed-bank
		P = present	Number of germinants
Senecio glomeratus	Asteraceae		12
Senecio glossanthus	Asteraceae		5
Silene nocturna	Caryophyllaceae		2
Sonchus oleraceus	Asteraceae		26
Ursinia anthemoides	Asteraceae	P	36
Vulpia myuros	Poaceae		51
Vulpia sp.	Poaceae		73
Wahlenbergia preissii	Campanulaceae		67
Ehrharta longiflora *	Poaceae	P	
		Total	1360
Unidentified			
Species 1	Asteraceae		892
Species 2			113
Species 3			16
Species 4			10
Species 5			6
Species 6			6
Species 7			3
Species 8			3
Species 9			1
Species 10			1
Species 11			1
Species 12			1
		Total	1053

* Annual or short-lived perennial

Appendix 2. Plant species in life-form categories from Franklandia Reserve, including above ground vegetation and numbers of soil seed-bank germinants. Nomenclature follows Paczkowska and Chapman (2000).

Species	Family	Above ground P = present	Soil seed-bank Number of germinants
Native species			
Trees			
Bradysporous			
Banksia attenuata	Proteaceae	P	5
Banksia grandis	Proteaceae	P	
Banksia ilicifolia	Proteaceae	P	
Melaleuca preissiana	Myrtaceae	P	
Xylomelum occidentale	Proteaceae	P	
Non-bradysporous			
Agonis flexuosa	Myrtaceae	P	
Eucalyptus marginata	Myrtaceae	P	
Corymbia calophylla	Myrtaceae	P	
Shrubs			
Bradysporous			
Allocasuarina humilis	Casuarinaceae	P	
Calothamnus lateralis	Myrtaceae	P	
Melaleuca thymoides	Myrtaceae	P	
Non-bradysporous			
Acacia sp.	Mimosaceae		1
Andersonia sp.	Epacridaceae		6
Calytrix sp.	Myrtaceae		2
Conostephium sp.	Epacridaceae		139
Eriostemon sp.	Rutaceae		7
Hibbertia sp.	Dilleniaceae		16
Kunzea sp.1	Myrtaceae		9
Kunzea sp.2	Myrtaceae		76
Leucopogon sp.	Epacridaceae		4
Stirlingia latifolia	Proteaceae	P	10
Myrtaceae sp.	Myrtaceae		5
Acacia extensa	Mimosaceae	P	
Acacia flagelliformis	Mimosaceae	P	
Acacia pulchella	Mimosaceae	P	
Acacia semitrullata	Mimosaceae	P	
Adenanthos meisneri	Proteaceae	P	
Adenanthos obovatus	Proteaceae	P	
Andersonia caerulea	Epacridaceae	P	
Astartea fascicularis	Myrtaceae	P	

Species	Family	Above ground P = present	Soil seed-bank Number of germinants
Boronia dichotoma	Rutaceae	P	
Bossiaea eriocarpa	Papilionaceae	P	
Calytrix flavescens	Myrtaceae	P	
Calytrix fraserii	Myrtaceae	P	
Comesperma calymega	Polygalaceae	P	
Conospermum capitatum	Proteaceae	P	
Conostephium preissii	Epacridaceae	P	
Daviesia physodes	Papilionaceae	P	
Eriostemon spicatus	Rutaceae	P	
Euchilopsis linearis	Papilionaceae	P	
Gompholobium capitatum	Papilionaceae	P	
Gompholobium tomentosum	Papilionaceae	P	
Hardenbergia comptoniana	Papilionaceae	P	
Hemiandra pungens	Lamiaceae	P	
Hibbertia racemosa	Dilleniaceae	P	
Hibbertia hypericoides	Dilleniaceae	P	
Hibbertia vaginata	Dilleniaceae	P	
Hovea trisperma	Papilionaceae	P	
Hypocalymma angustifolium	Myrtaceae	P	
Jacksonia sternbergiana	Papilionaceae	P	
Kunzea ericifolia	Myrtaceae	P	
Kunzea recurva	Myrtaceae	P	
Leucopogon australis	Epacridaceae	P	
Leucopogon oxycedrus	Epacridaceae	P	
Leucopogon polymorphus	Epacridaceae	P	
Leucopogon propinquus	Epacridaceae	P	
Lysinema ciliatum	Epacridaceae	P	
Pericalymma ellipticum	Myrtaceae	P	
Persoonia longifolia	Proteaceae	P	
Persoonia saccata	Proteaceae	P	
Petrophile linearis	Proteaceae	P	
Platytheca galiodes	Tremandraceae	P	
Scaevola striata	Goodeniaceae	P	
Stackhousia monogyna	Stackhousiaceae	P	
Herbs			
Perennial			
Above ground			
Burchardia sp.	Colchicaceae		1
Conostylis sp.	Haemodoraceae	P	7
Dampiera sp.	Goodeniaceae		3
Dasypogon bromeliifolius	Dasypogonaceae	P	2
Drosera pycnoblasta	Droseraceae		1

Species	Family	Above ground	Soil seed-bank
		P = present	Number of germinants
Lepidosperma sp.	Cyperaceae		1
Lomandra sp.	Dasypogonaceae		19
Platysace compressa	Apiaceae	P	1
Stylidium brunonianum	Stylidiaceae	P	1
Agrostocrinum scabrum	Anthericaceae	P	
Amphipogon turbinatus	Poaceae	P	
Anarthria prolifera	Restionaceae	P	
Burchardia congesta	Colchicaceae	P	
Caesia micrantha	Anthericaceae	P	
Chamaescilla corymbosa	Anthericaceae	P	
Dampiera linearis	Goodeniaceae	P	
Drosera paleacea	Droseraceae	P	
Drosera pulchella	Droseraceae	P	
Hypolaena exsulca	Restionaceae	P	
Lagenophora sp.	Asteraceae	P	
Lepidosperma costale	Cyperaceae	P	
Lepidosperma squamatum	Cyperaceae	P	
Lomandra nigricans	Dasypogonaceae	P	
Lomandra preissii	Dasypogonaceae	P	
Lomandra sericea	Dasypogonaceae	P	
Lyginia barbata	Restionaceae	P	
Patersonia occidentalis	Iridaceae	P	
Stylidium junceum	Stylidiaceae	P	
Stylidium piliferum	Stylidiaceae	P	
Stylidium repens	Stylidiaceae	P	
Stylidium schoenoides	Stylidiaceae	P	
Stylidium violaceum	Stylidiaceae	P	
Tricoryne elatior	Anthericaceae	P	
Xanthosia huegelii	Apiaceae	P	
Geophyte			
Drosera bulbosa	Droseraceae		8
Drosera macrantha	Droseraceae		3
Stylidium calcaratum	Stylidiaceae		1
Thysanotus patersonii	Anthericaceae	P	6
Drosera erythrorhiza spp. *erythrorhiza*	Droseraceae	P	
Drosera menziesii spp. *penicillaris*	Droseraceae	P	
Meeboldina coangustata	Restionaceae	P	
Thysanotus multiflorus	Anthericaceae	P	
Poly-ennial			
Anigozanthis manglesii	Haemodoraceae	P	1

Species	Family	Aboveground P = present	Soil seed-bank Number of germinants
Annual			
Centrolepis aristata	Centrolepidaceae		3
Centrolepis drummondii	Centrolepidaceae		42
Crassula colorata	Crassulaceae		111
Crassula sp.	Crassulaceae		1
Drosera glanduligera	Droseraceae	P	63
Hydrocotyle sp.	Apiaceae		2
Isolepsis cernua	Cyperaceae		44
Isolepsis ossarnus	Cyperaceae		1305
Lobelia sp.	Lobeliaceae		4
Millotia tenuifolia	Asteraceae		20
Phyllangium paradoxum	Loganiaceae		1
Quinetia urvillei	Asteraceae		7
Trachymene pilosa	Apiaceae		362
Trachymene cyanopetela	Apiaceae		10
Trachymene ornata	Apiaceae		39
Apiaceae sp.	Apiaceae		2
Lepidosperma longitudinale	Cyperaceae	P	
Orchids			
Diuris sp.	Orchidaceae		5
Leporella fimbriata	Orchidaceae	P	8
Caladenia flava	Orchidaceae	P	
Caladenia discoidea	Orchidaceae	P	
Caladenia latifolia	Orchidaceae	P	
Caladenia longicauda subsp. *clivicola*	Orchidaceae	P	
Caladenia vulgata	Orchidaceae	P	
Diuris corymbosa	Orchidaceae	P	
Elythranthera brunonis	Orchidaceae	P	
Eriochilus dilatatus	Orchidaceae	P	
Microtis media	Orchidaceae	P	
Pterostylis barbata	Orchidaceae	P	
Pterostylis recurva	Orchidaceae	P	
Pterostylis vittata	Orchidaceae	P	
Pterostylis aff *nana*	Orchidaceae	P	
Thelymitra crinita	Orchidaceae	P	
Thelymitra holmesii	Orchidaceae	P	
Cycad			
Macrozamia riedlei	Zamiaceae	P	
Grass Tree			
Xanthorrhoea brunonis	Xanthorrhoeaceae	P	
		Total	2364

Species	Family	Above ground P = present	Soil seed-bank Number of germinants
Non-native species			
Herbs			
Annual			
Aira caryophyllea	Poaceae		195
Aira cupaniana	Poaceae		22
Arctotheca calendula	Asteraceae		5
Briza maxima	Poaceae	P	140
Bromus sp.	Poaceae		6
Hypochaeris glabra	Asteraceae		9
Isolepsis marginata	Cyperaceae		71
Lolium rigidum	Poaceae		794
Oxalis corniculata	Oxalidaceae		16
Sonchus oleraceus *	Asteraceae		32
Sonchus sp. *	Asteraceae		2
Ursinia anthemoides	Asteraceae		22
Vulpia myuros	Poaceae		8
Vulpia sp.	Poaceae		5
Wahlenbergia pressii	Campanulaceae		11
Orchids			
Disa bracteata	Orchidaceae	P	4
		Total	1342
Unidentified			
Species 9			143
Species 4			40
Species 14			3
Species 15			2
Species 16			1
Species 17			1
Species 18			1
		Total	191

* Annual or short-lived perennial